Species' distribution models indicate contrasting late-Quaternary histories for southern and northern hemisphere bird species

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Abstract

Aim: To test hypotheses: that Fynbos species had more extensive distributions at the Last Glacial Maximum (LGM), extending onto the exposed 'Agulhas Plain'; that genetically distinct British taxa could have persisted through the LGM on adjacent areas of exposed shelf.

Location: Southern Africa; Europe.

Methods: Climatic response surfaces were fitted for 14 Fynbos and two European birds. These models were used to hindcast species' distributions for palaeoclimates simulated using a fully-coupled atmosphere–ocean general circulation model. LGM annual net primary productivities (ANPP) of two plant functional types upon which the European birds depend were simulated using a dynamic vegetation model and compared to potential LGM bird distributions.

Results: Fynbos birds' potential LGM distributions mostly extended southwards onto the exposed Agulhas Plain and consistently were more extensive than at present. This contrasts with conventional expectations for temperate species based upon northern hemisphere evidence. North-west European taxa potentially had LGM ranges on exposed shelf and ice-free areas west and south-west of the British Isles ice sheet. This is consistent with available genetic evidence, supporting the long-standing hypothesis that these taxa persisted through the LGM in this region. In both regions, results allow generation of new testable hypotheses about species' evolution and palaeobiogeography.

Main Conclusions: Bird species found today in Fynbos likely had more extensive ranges under glacial conditions, with many species' potential ranges extending onto the Agulhas Plain. Bird taxa today restricted to the British Isles probably survived the LGM with limited distributions on exposed shelf and ice-free areas south-west of the British Isles ice sheet. Areas of shelf exposed under glacial conditions are likely to have been important components of glacial distributions of species in both northern and southern hemispheres. The contrasting history of northern and southern hemisphere species has important conservation implications, especially in relation to conserving intra-specific genetic diversity.

Keywords

Fynbos endemic birds; South Africa; Agulhas Plain; peri-glacial survival; British Isles; *Loxia scotica*; *Lagopus lagopus scotica*; LPJ-GUESS; HadCM3; phylogeography.

1. Introduction

Species' distribution models (SDMs), relating species' present recorded distributions to present climatic conditions (Pearson & Dawson, 2003), are widely used to explore species' potential distributions under future climatic conditions projected using general circulation models (GCMs), first being applied in this way >15 years ago (Huntley *et al.*, 1995; Lenihan & Neilson, 1995). Only recently, however, have SDMs been used to explore species' potential past distributions under GCM-simulated palaeoclimatic conditions (Martínez-Meyer & Peterson, 2006; Garzon *et al.*, 2007; Carnaval & Moritz, 2008; Alba-Sanchez *et al.*, 2010), or to identify areas where species' may have persisted during periods of the late Quaternary when conditions were unfavourable for their wider occurrence (Buckley *et al.*, 2009; VanDerWal *et al.*, 2009). To a large extent this can be attributed to historical limitations of GCM palaeoclimatic simulations. Until recently, these predominantly were made using atmospheric GCMs that required sea surface temperatures (SSTs) to be specified, usually on the basis of summer and winter season reconstructions made from microfossil evidence (CLIMAP Project Members, 1984). Furthermore, neither ocean circulation nor seasonal sea-ice cover generally were simulated. Even when refined using a nested regional climate model (RCM), using the RCM output to drive palaeovegetation simulations revealed substantial biases with respect to the palynological record of past vegetation, (Huntley *et al.*, 2003). Similar biases were revealed when comparing simulated climates with conditions inferred from dated permafrost features (van Huissteden *et al.*, 2003). As Alfano *et al*. (2003) showed, these biases were likely a result largely of how reconstructed seasonal SSTs were used to derive an annual cycle of SSTs.

As computing power increased, however, and the imperative for more reliable projections of future climate drove the development of fully-coupled ocean–atmosphere GCMs, these models have also begun to be applied to simulate late Quaternary palaeoclimates. Singarayer and Valdes (2010) used a version of the Hadley Centre Unified Model to make a consistent set of simulations for a series of time slices extending back through the last glacial to the last interglacial. These simulations provide the basis for palaeovegetation simulations that are sufficiently robust to be used to supplement information from the palynological record, allowing exploration of the drivers of past forest dynamics (Miller *et al.*, 2008) and of the character and productivity of last glacial vegetation throughout northern Eurasia (Allen *et al.*, 2010).

Such series of GCM simulations provide a basis for applying SDMs to explore the late-Quaternary history of taxa that have a limited, or no, fossil record. They can also be used to explore how the different glacial palaeogeography, as a result of eustatic depression of sea-level by a maximum of *ca*. 120 m at the last glacial maximum (LGM; *ca*. 21 ka BP), may have been important in providing areas of distribution that are now submerged (Sakaguchi *et al.*, 2010). In addition, they are a potentially valuable basis for testing and generating hypotheses in historical biogeography. Here we illustrate this potential using SDMs fitted to bird species of two regions, southern Africa and north-west Europe, that provide several marked contrasts. In particular, southern Africa experienced no extensive development of last glacial ice sheets, whereas large parts of northern Europe and the European mountains were covered by ice sheets at the LGM (Ehlers & Gibbard, 2005). Prevalent climatic constraints also differ today between the two regions: Nowhere in north-west Europe experiences any significant degree of seasonal moisture deficiency, whereas much of the region is typified by sub-zero winter temperatures and snow cover even in the lowlands. In contrast, seasonal drought typifies most of southern Africa, whilst sub-zero temperatures and snow are features generally only of the higher mountains (e.g. Mulder & Grab, 2010).

Exploring how palaeoclimatic conditions potentially impacted upon species in these two regions allows us to examine whether the paradigm, based upon northern hemisphere evidence, of temperate species having more restricted glacial distributions applies also in the southern hemisphere. We also apply our SDMs to address two specific hypotheses:

- That LGM palaeoclimatic conditions enabled bird species associated today with the Fynbos Biome of southern and south-western South Africa to have more extensive LGM distributions, including southward range extensions onto the ‘Agulhas Plain’ that was exposed at that time.

- That species or races today restricted to the British Isles, including the endemic *Loxia scotica* (Scottish Crossbill) and *Lagopus lagopus scoticus* (Red Grouse), as well as the genetically distinctive *Pinus sylvestris* (Scots Pine) found today in Scotland (Ennos, 1997), could have persisted through the LGM on ice-free areas and areas of exposed continental shelf south-west of the British Isles (Huntley & Birks, 1983; Huntley, 1989).

2. Methods

To address the first hypothesis, we examined the 39 bird species listed by Hockey *et al*. (2005) as primarily associated with the Fynbos Biome. Fourteen species were selected (Table 1) on the basis that: (1) they are southern African endemics; (2) they do not range extensively beyond the Fynbos; and (3) they were mapped as individual taxa by Harrison *et al*. (1997). Distribution and reporting rate data, the latter a proxy for abundance, were mapped for southern African birds by Harrison *et al*. (1997) on a 0·25° grid, except in Botswana where a 0·5° grid was used. Reporting rate data for the 14 selected species were obtained from the Animal Demography Unit, University of Cape Town, and used to fit quantitative climatic response surface (CRS) models.

To address the second hypothesis, distribution data for *Loxia scotica* and *Lagopus lagopus* (Red / Willow Grouse), were obtained from the European Bird Census Council (EBCC). These data, mapped by Hagemeijer and Blair (1997), were recorded on a *ca*. 50 km grid. Unfortunately *L. l. scoticus*, endemic to the British Isles and distinguished from other sub-species principally by its uniform and seasonally invariant plumage and its diet principally of *Calluna vulgaris* (Ling) shoots (Cramp & Simmons, 1980), was not mapped separately. Qualitative CRSs were fitted using data for the entire area mapped by the EBCC.

CRS models describe species' recorded distributions or abundances in relation to a series of bioclimatic variables derived from present climatic data. Both the quantitative models for Fynbos species and the qualitative models for European species were fitted by locally-weighted regression following methods described by Huntley *et al* (1995; 2011). We favour this approach because: it requires an *a priori* choice of a limited number of biologically relevant bioclimatic variables; it makes no assumptions about the form of the relationships between species' probability of occurrence or abundance and the bioclimatic variables; it allows for interacting effects of bioclimatic variables and for these interactions to be non-stationary in climatic space; the fitted response surface is readily visualised, which is of great benefit in model interpretation; and extrapolation of the models into climatic space not represented in the training dataset is both conservative and predictable. Goodness-of-fit and robustness of the models were assessed using the measures and validation procedures described by Huntley *et al*. (2011). With the exception of species recorded from ≤25 grid cells, model validation was performed by fitting and testing models on 100 random

70:30 splits of the data; in the case of the more sparsely recorded species models were fitted omitting and predicting each grid cell in turn. Threshold values for determining suitable grid cells were taken as those values that maximised Cohen's kappa (Cohen, 1960; Huntley *et al.*, 1995).

Bioclimatic variables were derived from climatic variables in the CRU CL 1.0 0·5° dataset (http://www.cru.uea.ac.uk/~timm/grid/CRU_CL_1_0.html, New *et al.*, 1999) and/or the WorldClim 2·5′ dataset (http://www.worldclim.org/, Hijmans *et al.*, 2005). Bioclimatic variables used were chosen to reflect primary constraints on bird species' distributions and abundance, whether acting directly or indirectly. As discussed by Huntley *et al*. (2006), appropriate variables differ between the two regions: Coldest month mean temperature, annual thermal sum above a 5°C threshold and annual ratio of actual to potential evapotranspiration were used for European species, whereas for Fynbos species, coldest and warmest month mean temperatures, annual ratio of actual to potential evapotranspiration and a measure of the intensity of either the dry or wet season, according to which gave the better model for each species, were used. Calculation of the measures of dry and wet season intensity is described by Huntley *et al*. (2006).

Palaeoclimate scenarios used were derived from the series of simulations made by Singarayer and Valdes (2010) using the HadCM3 fully-coupled atmosphere–ocean GCM (Gordon *et al.*, 2000; Pope *et al.*, 2000). Whereas many simulations made with different GCMs are available for the LGM and Holocene 'optimum' (6 ka BP), this consistent series of 68 simulations spanning the past 120 ka offers a unique opportunity to explore species' potential distributions and abundances for a range of past conditions. Atmospheric composition, orbital forcing, ice-sheet extent and altitude, and the land–sea mask were prescribed, respectively, on the basis of ice-core data, orbital calculations, ice-sheet modelling and sea-level depression inferred from ice-volume evidence. Past values of climatic variables were derived from the GCM outputs following Allen *et al*. (2010), but were extended to include shelf areas exposed by eustatic sea-level depression. To do this we first calculated the potential present (i.e. 1961–90) climate of grid cells exposed by the maximum 120 m sea-level depression. This was achieved by fitting thin-plate spline surfaces (Hutchinson, 1989) relating each of the 36 relevant climatic variables from the CRU CL 1.0 dataset (i.e. 12 monthly means of temperature, precipitation and percentage cloud cover) concurrently to longitude, latitude and altitude. Climatic variables were then interpolated for shelf grid cells, altitudes for

which were calculated as means of the relevant grid cells in the GEBCO 1′ resolution global altitudinal and bathymetric grid (IOC *et al.*, 2003). Interpolated anomalies for the palaeoclimate scenario were then applied to these values, and finally bioclimatic variable values were calculated. Species' potential past distribution and/or abundance patterns were simulated using the CRS models. Potential late Quaternary distribution and/or abundance patterns were then mapped and compared with those simulated for the present.

To explore the extent to which *Pinus sylvestris* and *Calluna vulgaris*, specific food plants required by the two north-west European bird taxa, may have been present in western Europe at the LGM, and their likely productivity, we used results from a simulation of LGM vegetation north of 35° N made using the LPJ-GUESS dynamic vegetation model (Smith *et al.*, 2001). This simulation (Allen *et al.*, 2010) used 47 plant functional types (PFTs), including one parameterised to represent *P. sylvestris*. Although *C. vulgaris* was not specifically represented as a PFT, the PFT parameterised to represent dwarf shrubs in the Ericaceae can be taken as an adequate representation of this species because it is the dominant representative of this PFT in most areas where the PFT has high productivity. The principal advantages of this approach, rather than of fitting CRS models for the plant taxa and using them to simulate their LGM distributions, are: (1) that direct effects upon plant performance of the lower atmospheric CO_2 concentration at the LGM, compared to prior to the industrial revolution, are accounted for by LPJ-GUESS; and (2) that LPJ-GUESS provides quantitative simulations of annual net primary productivity (ANPP) for each PFT, whereas CRSs, and the data to which they could be fitted, provide only qualitative information about where the species potentially might occur. Details of the LGM palaeovegetation simulation, including boundary conditions used, are given by Allen *et al*. (2010).

3. Results

3.1 Fynbos birds

CRS models for the 14 species all gave goodness-of-fit measures indicating high performance, values for the area under the curve (AUC) for a receiver operating characteristic plot all being > 0·97 (Table 1). The models were also shown to be robust (for details see Huntley *et al.*, 2011). When used to simulate species' potential LGM distribution and abundance patterns, they revealed evidence supporting the

hypothesised southward range extensions onto exposed shelf areas, although with individualistic species' responses (Figure 1).

The species examined fall into four groups on the basis of their present distributions (see Supplementary Figure S1(a – d) for species' recorded and simulated potential present distributions). The first group comprises seven species at present limited to a greater or lesser extent to Western Cape (see Supplementary Information Figure S2 for place names referred to in the text) and adjacent parts of the surrounding provinces (*Pternistis capensis* (Cape Spurfowl), Figure 1(a); *Chaetops frenatus* (Cape Rock-jumper), Figure 1(c); *Cryptillas victorini* (Victorin's Warbler), Figure 1(f); *Promerops cafer* (Cape Sugarbird), Figure 1(g); *Anthobaphes violacea* (Orange-breasted Sunbird), Figure 1(i); *Crithagra totta* (Cape Siskin), Figure 1(k); and *C. leucopterus* (Protea Seedeater), Figure 1(n)). These species generally had much enlarged potential LGM ranges, extending eastwards, northwards and also southward onto the Agulhas Plain, although in the case of *Chaetops frenatus* and *Cryptillas victorini* extension onto the Agulhas Plain is simulated only in the east of their potential LGM ranges.

Three species have present distributions confined largely to the east, often principally in the Drakensberg and surrounding mountainous areas (*Chaetops aurantius* (Drakensberg Rock-jumper), Figure 1(d); *Promerops gurneyi* (Gurney's Sugarbird), Figure 1(h); and *Crithagra symonsi* (Drakensberg Siskin), Figure 1(l)). All three had potential LGM distributions of increased extent, with increases especially towards the north and, to a lesser extent, east. Southward range extension was limited, with potentially suitable grid cells on the Agulhas Plain an order of magnitude further from the species' principal potential range (500 – 1000 km) than typical dispersal distances observed for Fynbos species, and thus unlikely to have been occupied.

A further three species have more widespread present distributions (*Geocolaptes olivaceus* (Ground Woodpecker), Figure 1(b); *Cinnyris afer* (Greater Double-collared Sunbird), Figure 1(j); and *Crithagra scotops* (Forest Canary), Figure 1(m)). All three again had potentially more extensive LGM distributions, extending in almost all directions, including southwards onto the Agulhas Plain. In two cases they exhibited a tendency potentially to retreat from more inland parts of their present range, the exception being *G. olivaceus* that potentially also expanded its range inland.

For several species in these groups, suitable conditions are simulated at the LGM also in markedly disjunct areas far to the north or north-east of the remainder of the species' potential LGM range, notably in northern Namibia and/or South Africa. Given their isolation, it is unlikely, albeit not impossible, that such areas would have been occupied.

The final species, *Bradypterus sylvaticus* (Knysna Warbler), Figure 1(e), has a very restricted present distribution close to the south coasts of Western and Eastern Cape. Although at 0·5° resolution the CRS model simulates rather few occurrences, these are in the appropriate areas. At the LGM the species' distribution is simulated to shift eastwards and also to extend southwards onto the narrow shelf areas south of Eastern Cape. Interestingly, however, there is no suggestion of any extension northwards, in contrast to what is seen for most other species.

Median range extent for the 14 species, calculated as the number of grid cells simulated as potentially suitable, is *ca*. 2·6 x greater for LGM climate than for present climate. Only one species, *Crithagra scotops*, has a potential LGM range virtually identical in extent to that for the present, whilst three species (*Chaetops frenatus*, *Cryptillas victorini* and *Crithagra leucopterus*) have potential LGM range extents ≥ 4 x those simulated for the present. These LGM results can be placed in context by considering simulations made for palaeoclimate scenarios derived from simulations made by Singarayer and Valdes (2010) for a series of other past intervals (6, 9, 12, 15, 18, 42 and 120 ka BP, and three Heinrich Events (Andrews, 1998): H1 (17 ka BP), H2 (24 ka BP) and H4 (38 ka BP)) (see Supplementary Information, Figures S2 – 15). These reveal that glacial palaeoclimates generally result in simulated range extents greater than at present, the most extreme potential range increases being simulated for Heinrich Event palaeoclimates. The latter all give median range extents > 4 x those simulated for the present, H1 (*ca*. 17k BP) with a median range extent of 5·6 x, being the most extreme. Strikingly, the last interglacial palaeoclimate (120 ka BP) was the only one to give a reduction, albeit marginally, in median range extent. Species most reduced in potential range at that time compared to the present were *Promerops gurneyi* (0·53), *Chaetops aurantius* (0·63) and *Crithagra symonsi* (0·67), the three species with present distributions principally in the Drakensberg and other mountainous eastern areas.

3.2 North-west European birds and their habitats

CRS models for both species had excellent goodness-of-fit measures (Table 2). That for *Loxia scotica* accurately simulated the species' distribution in Scotland (see Supplementary Figure S17 for the species' recorded distribution), although also simulating one grid square in England and two in Norway as potentially suitable under present climatic conditions (Figure 2(a)). For the LGM the species is simulated potentially to occupy a series of grid cells south-west of the ice sheet that covered most of the British Isles. In addition, areas in the Cantabrian mountains and eastern Pyrenees are simulated as potentially suitable, along with isolated grid cells in Cornwall and Brittany. Persistence of the species in these areas would have required presence of *Pinus*, preferably *P. sylvestris*, its principal food plant. As Figure 2(c) illustrates, simulated ANPP for the *P. sylvestris* PFT at the LGM is high in the areas simulated as potentially suitable for *L. scotica*. Most importantly, high ANPP of *P. sylvestris* is simulated throughout the exposed shelf and ice-free continental areas west and south-west of the British Isles ice sheet.

The model for *Lagopus lagopus* accurately simulates the species' present range that includes Britain and Ireland (*L. l. scoticus*) and the Boreal zone, its range in the latter extending from western Norway (*L. l. variegatus*) eastwards across Fennoscandia and northern Russia (*L. l. lagopus*) to Siberia and Boreal North America (see Supplementary Figure S17 for the species' recorded north-west European distribution). In addition, however, areas in the Alps, and a single grid cell in the Pyrenees, remote from the species' present range, are simulated as suitable for the species under present climatic conditions. The potential range simulated for the LGM extends throughout ice-free areas of the exposed shelf and British Isles, as well as across the southern North Sea basin and southwards through eastern Europe. In addition, most of the Cantabrians, parts of the Pyrenees, the Massif Central and the margins of the Alps are simulated as potentially suitable. Strikingly, the ice-free area of shelf north-east of Scotland also is simulated as potentially suitable, whilst the area of suitable conditions is constricted in central southern England, with highly suitable conditions to west and east but only a limited link between the two where conditions are less suitable.

Whereas most *Lagopus lagopus* sub-species feed primarily upon *Salix* (Willow) and *Betula* (Birch) catkins and buds, or on berries of various dwarf shrubs, including *Vaccinium* spp. (Bilberry, Cowberry, etc.) and *Empetrum nigrum* (Crowberry), *L. l. scoticus* feeds primarily upon *Calluna vulgaris* shoots.

Accordingly, the key habitat requirement for the latter sub-species is presence of *Calluna*-dominated heathlands and related communities. The most relevant PFT simulated by Allen *et al*. (2010) is the Ericaceae (dwarf shrub) PFT, parameterisation of which results in behaviour similar to that of *C. vulgaris* in terms of the ANPP pattern simulated for present climate. Simulated ANPP for this PFT for the LGM (Figure 2(d)) is high on the exposed shelf and land areas to the west and south-west of the British Isles. It is also high in northern Iberia, around the Massif Central and western Alps, in the southern North Sea and in parts of eastern Europe. The coincidence between the high productivity area simulated to the south-west of the British Isles and the high suitability of the same area for *L. lagopus* provides additional support for the hypothesis that *L. l. scoticus* persisted in this region through the LGM.

4. Discussion

On the basis of northern hemisphere evidence, there is a paradigm expectation that temperate species' ranges were reduced in extent under glacial conditions, species being constrained to what frequently are referred to as 'glacial refugia'. Simulated LGM ranges of Fynbos species, however, are generally more extensive, or at least no less extensive, than those simulated for present climatic conditions. This reflects the absence of extensive continental ice sheets or mountain glaciation in southern Africa (Boelhouwers & Meiklejohn, 2002), coupled to limited cooling and reduced spatial extent of the summer rainfall regime, the latter likely associated with a general reduction in monsoon strength under glacial conditions. This potential for more, rather than less, extensive LGM ranges has important implications for Fynbos species, and perhaps also for other southern hemisphere temperate species. In particular, present distributions and populations of Fynbos species are likely reduced compared to their ranges and populations during most of the Pleistocene, perhaps rendering them even more vulnerable than northern hemisphere temperate species to the impacts of projected future climatic changes. The overall range reduction simulated for the last interglacial serves to underline this issue. That this reduction was potentially most severe for species of the eastern mountains provides a striking parallel to simulated impacts of projected future climatic changes upon species with this general distribution (Huntley *et al.*, 2011; Huntley & Barnard, submitted).

Our results for most of the 14 Fynbos species modelled also uphold our hypothesis that these species' more extensive LGM ranges would have included areas on the exposed Agulhas Plain. Given the

paradigm expectation that temperate species' ranges shifted equatorward during glacial stages, the overall southward shift of potential range at the LGM exhibited by several species is striking. This expectation arises primarily from evidence for northern hemisphere regions where seasonal temperatures are a principal determinant of species' range limits. In South Africa, however, remoteness from any sea-ice cover at the LGM, even in winter, and persistence of the warm Agulhas Current during glacial stages (Gersonde *et al.*, 2003), even if somewhat weakened (Franzese *et al.*, 2006), would have limited the degree of cooling. Furthermore, the differing seasonal patterns of precipitation and drought, with winter rains predominating in the south-west but summer rains in the east (see e.g. South Africa Rain Atlas, http://134.76.173.220/rainfall/index.html), are of much greater importance in determining species' present distribution patterns (Cowling *et al.*, 1997). Changes in seasonal precipitation patterns thus are likely to have been at least as important as, if not more important than, temperature changes in driving species' range changes in this region during the Pleistocene. The general potential range expansion of Fynbos species associated with the region of predominantly winter rainfall is consistent with projections of increased winter rainfall in the region at the LGM (see e.g. PMIP2 results, http://pmip2.lsce.ipsl.fr/).

Centres of diversity in the northern hemisphere temperate zone, in terms of both species richness and intra-specific genetic diversity, frequently are associated with the limited areas in which species of this zone occurred during the LGM (Hampe & Petit, 2005). Fynbos species, however, potentially experience their greatest range restriction under peak interglacial conditions, with the most extreme recent 'bottle-neck' being during the last interglacial. We can thus hypothesise that both the species richness of Fynbos species and their intra-specific genetic diversity should be greatest in their potential 'interglacial refugia'. We also postulate that closely related species pairs with vicariant distributions centred in the Western Cape and the eastern mountains, especially the Drakensberg (e.g. *Chaetops frenatus* / *C. aurantius*, *Promerops cafer* / *P. gurneyi*, *Crithagra totta* / *C. symonsi*) likely diverged from common ancestors as a consequence of isolation in these two 'refugial' regions, most probably during successive Pleistocene interglacials but alternatively during the early Pleistocene when glacial cooling was less strongly expressed.

To-date, Fynbos birds have attracted little attention from geneticists and phylogeographers. The results of our simulations, however, suggest a number of specific testable hypotheses, as well as the general hypotheses outlined above, that could be addressed using genetic approaches. For example,

315 species of the eastern mountains, whose potential last interglacial ranges are simulated to have been
316 particularly reduced, might be hypothesised to show genetic evidence of a more marked 'bottleneck' at that
317 time. Given that the majority of species potentially had increased range extents and populations during
318 the LGM, they can be expected to show population genetic evidence of recent contraction of both range
319 and population. The simulated potential suitability of disjunct areas at the LGM for species that have
320 vicariant sister species (e.g. *Chaetops frenatus* and *C. aurantius*, *Promerops cafer* and *P. gurneyi*) whose
321 LGM range potentially overlapped with, or was at least adjacent to, these disjunct areas, raises an
322 intriguing possibility. If these disjunct potential LGM range components were occupied, then there may be
323 a genetic legacy of inter-breeding in populations of the sister species if, as a result of their relatively recent
324 origins, the species were not by then completely isolated.

325 In the case of the hypothesised LGM survival on areas of exposed shelf and ice-free continent south-
326 west of the British Isles of taxa such as the endemic *Loxia scotica*, the Scottish genetic variant of *Pinus*
327 *sylvestris*, *Lagopus lagopus scoticus* and *Calluna vulgaris*, the simulations provide compelling supporting
328 evidence. Palaeoecological evidence long ago pointed to the likelihood of survival of *P. sylvestris* in this
329 region (Huntley & Birks, 1983; Birks, 1989), a hypothesis subsequently supported by genetic evidence
330 (Ennos, 1997; Sinclair *et al.*, 1998; Sinclair *et al.*, 1999; Kinloch *et al.*, 1986). Survival of this species
331 would imply survival of communities similar to those in which it is found today, such communities often
332 having an understorey in which *C. vulgaris* is a dominant species, even close to the north-westernmost limit
333 of *P. sylvestris* today in northern Norway (Jalas & Suominen, 1973) that closely coincides with the northern
334 limit of *C. vulgaris* in the same region (Gimingham, 1960). In this case the genetic evidence (Rendell &
335 Ennos, 2002) also points to the glacial survival of *C. vulgaris* in northern Europe, consistent with the model
336 evidence of areas of high ANPP of the Ericaceae (dwarf shrub) PFT south-west of the British Isles ice
337 sheet at the LGM.

338 Although the status of the endemic Scottish Crossbill has long been debated, it is now accorded
339 specific status as *Loxia scotica*. It is considered most closely related to *L. pytyopsittacus* (Parrot Crossbil),
340 another *Pinus* specialist, rather than to *L. curvirostra* (Common Crossbill) that generally specialises upon
341 *Picea* (Spruce). Although Knox (1989) speculated that *L. scotica* may have originated as recently as the
342 Holocene, from a population of *L. pytyopsittacus* that reached the British Isles during the Pleistocene and

subsequently became isolated, the simulation of suitable conditions for the species south-west of the British Isles ice sheet at the LGM suggests that the species may have a longer history. Furthermore, the simulated potential range at 120 ka BP, during the last interglacial, is closely similar to that occupied during the Holocene, leading us to hypothesise that the species has a history extending back at least to the that time, and perhaps much further into the Pleistocene. Such an hypothesis is amenable to testing using genetic evidence.

The status of *Lagopus lagopus scoticus* is similarly the subject of debate. Genetic evidence, however, suggests that this taxon is as distinct from other races of *L. lagopus* as is *L. lagopus* from *L. mutus* (Ptarmigan) in Scandinavia (Quintela *et al.*, 2010). The simulation of an extensive potential range for *L. lagopus* south-west and south of the British Isles ice sheet at the LGM, the near isolation of this area from other areas simulated as potentially suitable for *L. lagopus* at the LGM, and the coincidence that this area also is simulated to have a high ANPP for the Ericaceae (dwarf shrub) PFT at the LGM, together support the proposition that *L. l. scoticus* originated no later than the LGM, and potentially earlier in the late Pleistocene. The genetic evidence indicates that divergence between *L. l. scoticus* and *L. l. lagopus* occurred between 12,500 and 125,000 years ago (Quintela *et al.*, 2010). Such a divergence time would be consistent with an origin for *L. l. scoticus* as a result of isolation during the last glacial stage, and hence with the simulated range for *L. lagopus* at the LGM. That the population from which *L. l. scoticus* evolved was isolated also in an area with high ANPP of the Ericaceae (dwarf shrub) PFT might well have contributed to the evolution of the sub-species' dietary specialisation.

The simulated potential LGM range of *L. lagopus* also includes an isolated area of suitable conditions north-east of Scotland. This leads us to hypothesise that *L. l. variegatus* may have originated in this region during the last glacial stage, shifting to its present range in south-west Norway as the Scandinavian ice sheet retreated. Genetic evidence could again test this hypothesis.

Our simulations have provided support for both of our specific hypotheses, and have also led to the important conclusion that, in contrast to northern hemisphere temperate species, Fynbos species, and potentially also other southern hemisphere temperate species, potentially had LGM distributions that were more extensive than their present distributions. In the case of the north-west European species, available genetic evidence is consistent with our results and conclusions. These results also lead to new

hypotheses about the time of origin of *Loxia scotica* and the place and time of origin of both *Lagopus lagopus scoticus* and *L. l. variegatus*, all of which could be tested by new genetic data. In the case of the Fynbos species, our results also enable us to generate hypotheses that could be tested using new genetic evidence. From a biodiversity conservation viewpoint, and in the context of anthropogenic climatic change, the contrasting history of northern and southern hemisphere temperate species has important implications: Whereas it has been argued that "the rear edge matters" (Hampe & Petit, 2005) in relation to conserving intra-specific genetic diversity of northern hemisphere temperate species, almost the opposite may be true for southern hemisphere species if climatic change parallels previous interglacial maxima in terms of the resulting range restriction.

As Nogues-Bravo (2009) has argued, this and similar studies have limitations in terms of the assessment of uncertainties. This largely reflects a lack of means adequately to quantify the many sources of uncertainty, and thus realistically to assess the overall uncertainty of simulated distributions. These studies, nonetheless, are valuable because of their capacity to generate testable hypotheses. Improvements in modelling approaches, realistic assessments of uncertainties, and iterative interactions with other approaches together can advance our understanding of how species responded to past climatic changes. This is especially true of genetic approaches, and where taxa are poorly represented in the fossil record, such as most birds, and/or indistinguishable in the fossil record, such as the genetic races of *Pinus sylvestris*. Such advances are crucial to improving our ability to predict the consequences of present and projected future climatic changes.

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Biosketch

Brian Huntley is a palaeoecologist, ecologist and biogeographer with research interests in the interactions between species, ecosystems and their changing environment. His current work spans a range of taxonomic groups and ecosystems, from conifers forming New Zealand treelines to extinct Pleistocene mammals of Eurasia, although he has a particular interest in birds and climatic change. Judy Allen is a palaeoecologist with particular interests in Quaternary vegetation history. Phoebe Barnard is a conservation biologist with a particular interest in birds of the Fynbos Biome. Yvonne Collingham is a biologist who researches the responses of species to climatic changes. Phyllida Holliday is a biologist who is currently researching the history of the distributions of *Loxia* spp. worldwide.

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SUPPLEMENTARY MATERIAL

The online supplementary material comprises 17 Figures as follows:

Figure S1: Recorded and simulated distributions of 14 Fynbos bird species.

Figure S2: Map of southern Africa showing South African province names and neighbouring countries as referred to in the text.

Figures S3 – S16: Potential distributions for the present, 6, 9, 12, 15, 18, 21, 42 and 120 ka BP, and for Heinrich Events H1 (17 ka BP), H2 (24 ka BP) and H4 (38 ka BP), for 14 Fynbos bird species.

Figure S17: Recorded breeding distributions of *Loxia scotica* and *Lagopus lagopus* in north-west Europe.

Tables

Table 1: Goodness-of-fit of models fitted to the full data for Fynbos species

Scientific name	Common name	No. of grid cells from which recorded[1]	Goodness-of-fit of the climatic response surface model		
			AUC[2]	TSS[3]	K[4]
Pternistis capensis	Cape Spurfowl	207	0·973	0·817	0·775
Geocolaptes olivaceus	Ground Woodpecker	484	0·973	0·839	0·730
Chaetops frenatus	Cape Rock-jumper	50	0·993	0·957	0·635
C. aurantius	Drakensberg Rock-jumper	80	0·997	0·971	0·796
Bradypterus sylvaticus	Knysna Warbler	25	0·992	0·950	0·529
Cryptillas victorini	Victorin's Warbler	58	0·996	0·970	0·712
Promerops cafer	Cape Sugarbird	134	0·992	0·918	0·822
P. gurneyi	Gurney's Sugarbird	93	0·982	0·897	0·682
Anthobaphes violacea	Orange-breasted Sunbird	123	0·993	0·925	0·810
Cinnyris afer	Greater Double-collared Sunbird	464	0·984	0·877	0·793
Crithagra totta	Cape Siskin	118	0·992	0·927	0·754
C. symonsi	Drakensberg Siskin	49	0·999	0·984	0·867
C. scotops	Forest Canary	195	0·986	0·918	0·733
C. leucopterus	Protea Seedeater	69	0·992	0·916	0·710

[1] The number of 0·25° grid cells from which the species was recorded as present in the Southern African Bird Atlas Project dataset (Harrison *et al.*, 1997).

[2] Area under the curve for a receiver operating characteristic plot (Metz, 1978).

[3] True skill statistic (Allouche *et al.*, 2006).

[4] Cohen's kappa (Cohen, 1960; Monserud & Leemans, 1992).

564 **Table 2: Goodness-of-fit of models fitted to the full data for North-west European species**

Scientific name	Common name	No. of grid cells from which recorded[1]	Goodness-of-fit of the climatic response surface model		
			AUC[2]	TSS[3]	K[4]
Lagopus lagopus	Willow / Red Grouse	552	0·995	0·956	0·899
Loxia scotica	Scottish Crossbill	14	0·998	0·993	0·800

565

566 [1] The number of *ca*. 50 km grid cells from which the species was recorded as present in the
567 European Bird Census Council dataset (Hagemeijer & Blair, 1997).

568 [2] Area under the curve for a receiver operating characteristic plot (Metz, 1978).

569 [3] True skill statistic (Allouche *et al.*, 2006).

570 [4] Cohen's kappa (Cohen, 1960; Monserud & Leemans, 1992).

Figures

Figure 1: Potential distributions and abundances of Fynbos birds at the last glacial maximum

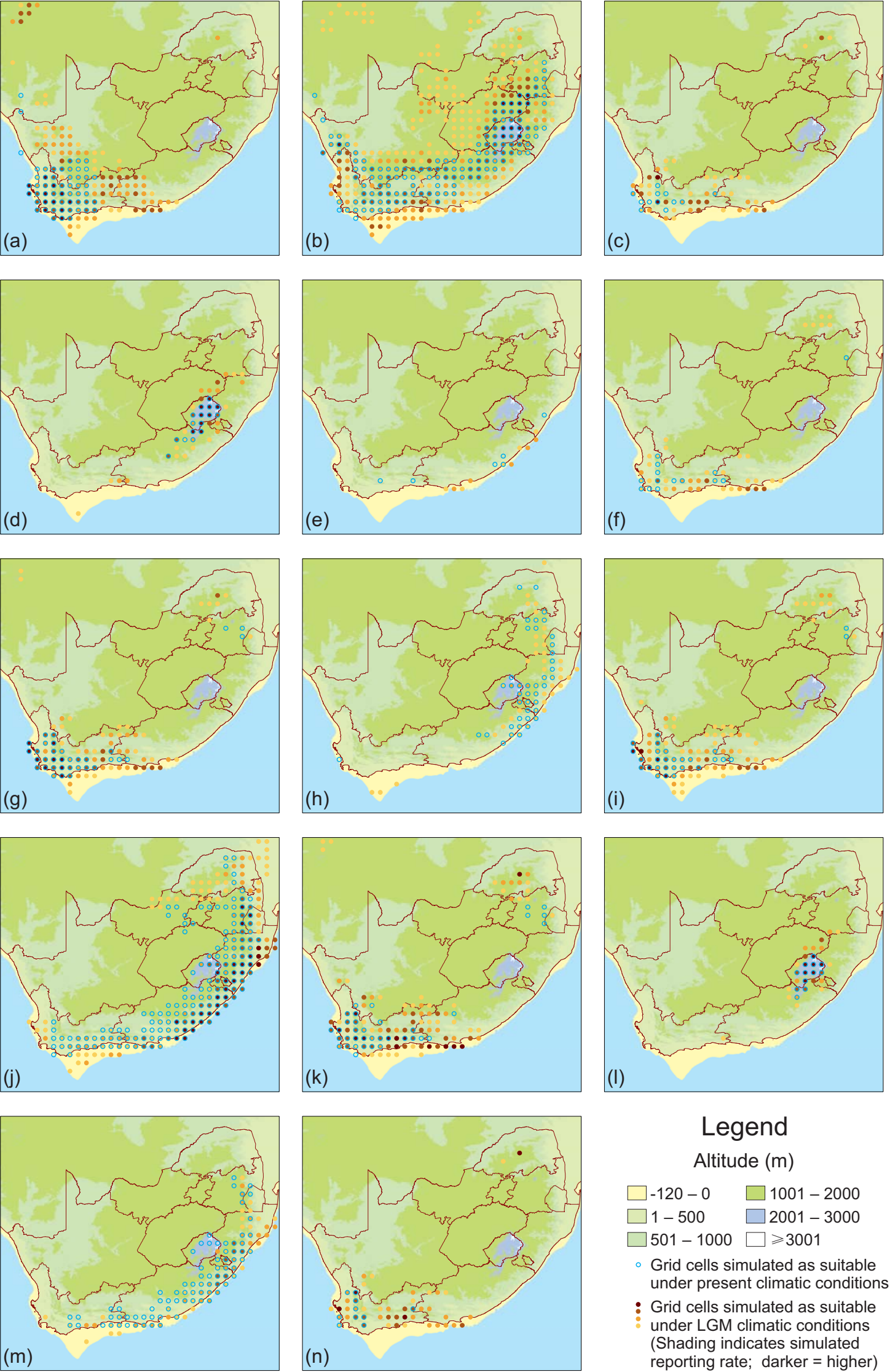
On each panel cyan rings indicate 0·5° grid cells simulated as potentially occupied under present climatic conditions, whilst shaded dots indicate cells potentially occupied at the LGM, darker shading indicating higher simulated reporting rates; cells simulated as suitable under both sets of climatic conditions have a shaded dot enclosed by a cyan ring. (a) *Pternistis capensis* – Cape Spurfowl; (b) *Geocolaptes olivaceus* – Ground Woodpecker; (c) *Chaetops frenatus* – Cape Rock-jumper; (d) *Chaetops aurantius* – Drakensberg Rock-jumper; (e) *Bradypterus sylvaticus* – Knysna Warbler; (f) *Cryptillas victorini* – Victorin's Warbler; (g) *Promerops cafer* – Cape Sugarbird; (h) *P. gurneyi* – Gurney's Sugarbird; (i) *Anthobaphes violacea* – Orange-breasted Sunbird; (j) *Cinnyris afer* – Greater Double-collared Sunbird; (k) *Crithagra totta* – Cape Siskin; (l) *C. symonsi* – Drakensberg Siskin; (m) *C. scotops* – Forest Canary; (n) *C. leucopterus* – Protea Seedeater.

Topography, including the approximate extent of exposed areas of continental shelf, is shown using the GEBCO 1′ resolution global altitudinal and bathymetric grid (IOC *et al.*, 2003).

Figure 2: Potential last glacial maximum distributions and ANPP of north-west European species

On the upper panels cyan rings indicate 0·5° grid cells simulated as potentially occupied under present climatic conditions, whilst shaded dots indicate cells potentially occupied at the LGM, darker shading indicating higher simulated probability of occurrence; cells simulated as suitable under both sets of climatic conditions have a shaded enclosed by a cyan ring. (a) *Loxia scotica* – Scottish Crossbill; (b) *Lagopus lagopus* (Red Grouse / Willow Grouse). The lower panels show ANPP (g C m^{-2} yr^{-1}) simulated by the LPJ-GUESS dynamic vegetation model for the LGM, darker shaded dots indicating higher productivity. (c) *Pinus sylvestris* – Scots Pine; (d) Ericaceae (dwarf-shrub) – Heaths, Ling.

Topography, including the approximate extent of exposed areas of continental shelf, is shown using the GEBCO 1′ resolution global altitudinal and bathymetric grid (IOC *et al.*, 2003). LGM ice sheet extents, indicated in blue-white, after Ehlers and Gibbard (2005).


(a)
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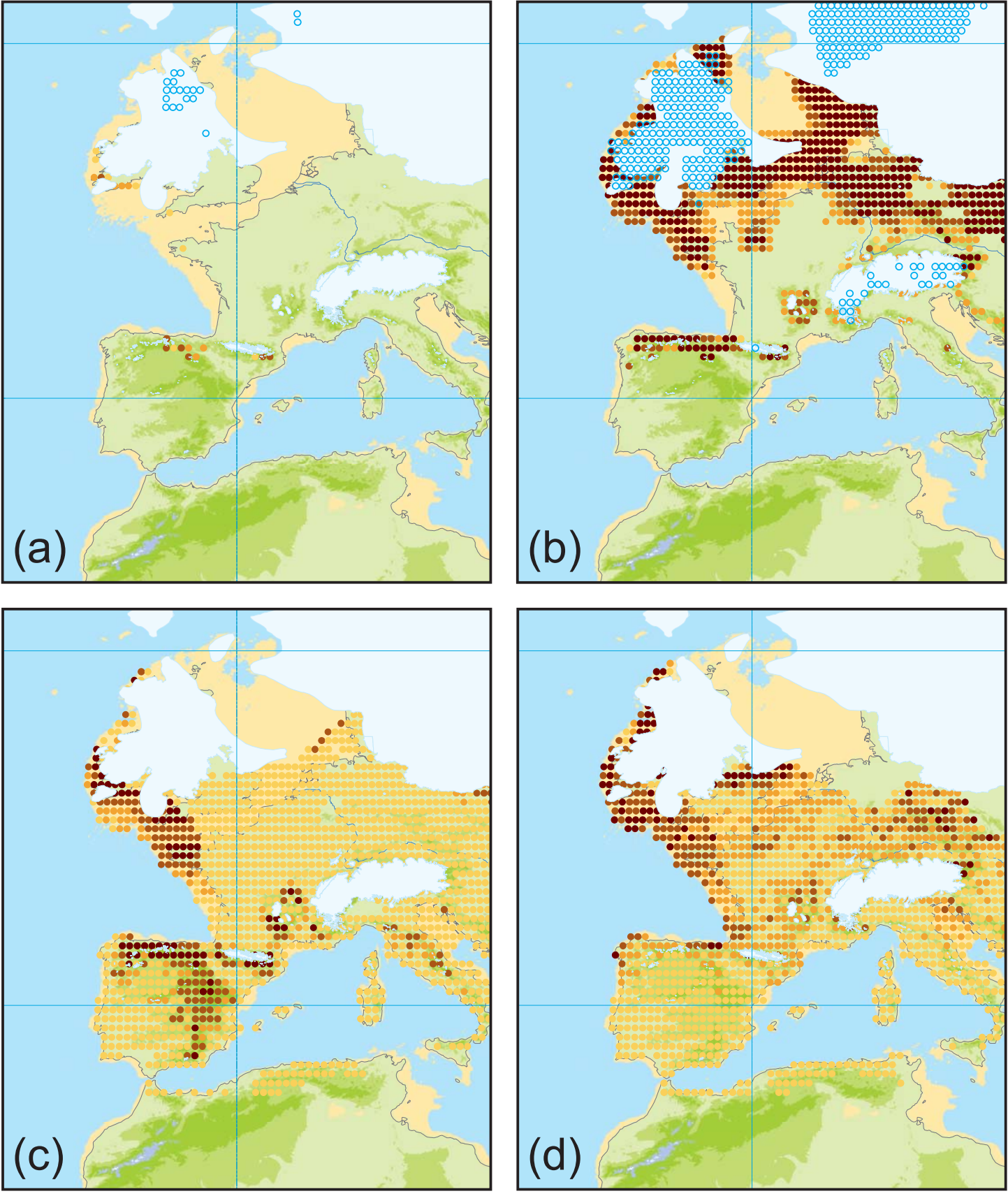
(n)
Legend
Altitude (m)
-120 – 0
1 – 500
501 – 1000
1001 – 2000
2001 – 3000
⩾3001
Grid cells simulated as suitable under present climatic conditions
Grid cells simulated as suitable under LGM climatic conditions (Shading indicates simulated reporting rate; darker = higher)



Legend

Pinus sylvestris ANPP (g C m^{-2} yr^{-1})

- < 50
- 51 – 100
- 101 – 200
- > 200

Altitude (m)

- -120 – 0
- 1 – 500
- 501 – 1000
- 1001 – 2000
- 2001 – 3000
- ⩾3001
- Ice sheets

Ericaceae (dwarf shrub) ANPP (g C m^{-2} yr^{-1})

- < 10
- 11 – 25
- 26 – 50
- > 50